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BAT PREDATION BY LONG-EARED OWLS IN MEDITERRANEAN AND TEMPERATE REGIONS OF SOUTHERN EUROPE

ANA MARÍA GARCÍA[1]
IMEDEA (CSIC-UIB), Miquel Marquès 21, E-07190 Esporles, Mallorca, Spain

FRANCISCO CERVERA
C.R.F. Granja de El Saler, Conselleria de Territori i Habitatge, Avda. dels Pinars 106, E-46012, Valencia, Spain

ALEJANDRO RODRÍGUEZ
Department of Applied Biology, Estación Biológica de Doñana, CSIC, Avda. María Luisa s/n, E-41013, Sevilla, Spain

ABSTRACT.—We described spatial and temporal variation in bat consumption by Long-eared Owls (*Asio otus*) at a coastal site of eastern Spain and examined the importance of bats in the diet of this raptor in nine temperate and 21 Mediterranean localities of southern Europe. In our study site in Spain, bats accounted for 2% of prey items, which is the largest percentage so far reported for the species. The vast majority of bats were *Pipistrellus* spp. Bat predation occurred in all seasons, but was significantly higher in spring and summer. The temporal pattern of bat predation was unrelated to temporal variation in the consumption of rodents, the dominant prey in the diet. Although a consistent increase in bat intake only in years of rodent scarcity predicts an aggregation of occurrences over time, bat occurrence during 31 successive seasons was not different from a random sequence. Pellets containing bat remains originated mainly from one communal roosting site. Bat remains appeared in pellets from five of 16 nests, accounting for 17% of prey items on average. In southern Europe, bats occurred in 38% of diets in the Mediterranean region, while they were absent in diets from adjacent temperate localities. Our results suggest that Long-eared Owls prey on bats rarely and opportunistically in Mediterranean sites, but also that bat aggregations could be a locally important food source for some individual owls during certain periods.

KEY WORDS: *Long-eared Owl;* Asio otus; *Chiroptera; diet; Mediterranean basin; trophic plasticity.*

PREDACIÓN DE MURCIÉLAGOS POR EL BÚHO CHICO EN REGIONES TEMPLADAS Y MEDITERRÁNEAS DEL SUR DE EUROPA

RESUMEN.—Describimos la variación espacial y temporal en el consumo de murciélagos por parte del búho Chico *Asio otus* en una localidad costera del este de España, y examinamos la importancia de los quirópteros en la dieta de esta rapaz en 30 localidades del sur de Europa, 9 de clima templado y 21 de clima mediterráneo. En nuestra área de estudio, los quirópteros constituyeron el 2% de las presas ingeridas, cifra que representa el mayor consumo conocido para la especie. Casi todos los murciélagos consumidos fueron a *Pipistrellus* spp. Su predación se produjo en todas las estaciones, pero fue significativamente más alta en primavera y verano. El patrón temporal de predación de murciélagos no estuvo relacionado con la variación temporal en el consumo de roedores, la presa dominante en la dieta. El incremento en el consumo de murciélagos sólo en años en los que los roedores son escasos predice una agregación temporal de las apariciones. Sin embargo, la presencia de murciélagos en la dieta a lo largo de 31 estaciones sucesivas no difirió de una secuencia aleatoria. La mayor parte de las egagrópilas que contuvieron murciélagos procedieron del dormidero comunal. Encontramos restos de quirópteros en cinco de los 16 nidos muestreados, donde constituyeron en promedio el 17% de las presas. En Europa meridional, los murciélagos aparecieron en el 38% de las dietas de la región mediterránea, pero en ninguna de las dietas de la región templada adyacente. Nuestros resultados indican que *A. otus* consume murciélagos con baja frecuencia y de forma oportunista en la región mediterránea, pero también sugieren que las agrupaciones de quirópteros pueden ser una fuente de alimento localmente importante para algunos individuos durante periodos concretos.

[Traducción del autor]

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[1] Email address: panamel@ono.com

Throughout the boreal and temperate regions of Europe, Long-eared Owls (*Asio otus*) prey almost exclusively upon microtine rodents (Herrera and Hiraldo 1976, Lundberg 1979, Marks et al. 1999). As a result, owl numbers decrease locally with declining vole (*Microtus* spp.) populations and, at larger spatial scales, owls may use nomadic or irruptive movements to track peaks in vole abundance (Lundberg 1979, Korpimäki 1985, Hanski et al. 1991). Such a numerical response is a trait of specialist predators that may be explained in part by low availability of alternative prey (Weber et al. 2002) and by high predictability of vole population peaks in such ecosystems (Korpimäki 1985). However, Long-eared Owls seem to depend less on rodents at lower latitudes (Bertolino et al. 2001), especially in Mediterranean regions (García and Cervera 2001) which feature lower environmental predictability, resulting in strong seasonal and annual fluctuations in the abundance of rodents and other prey (Blondel and Aronson 1999). Indeed diet diversification with decreasing latitude may be a general pattern in nocturnal raptors (Herrera and Hiraldo 1976, Mikkola 1983, Korpimäki and Marti 1995) and other predators (Revilla and Palomares 2002, Clavero et al. 2003), suggesting that specialization may not always reflect species-specific constraints in physiology or morphology, but behavioral flexibility (Futuyma and Moreno 1988, Martín et al. 1995).

Bats have regularly been reported, albeit in small amounts, as prey of a variety of diurnal and nocturnal raptors (e.g., Baker 1962, Ruprecht 1979, Barclay et al. 1982). Long-eared Owls are no exception. For example, in the British Isles, this species was the second most important bat predator among raptors (Speakman 1991). In this paper, we describe the pattern of bat consumption by Long-eared Owls during an 8-yr period in a Mediterranean site with good habitat for bats in terms of roost (buildings) and food availability (insects in rice fields and other flooded areas). We also review European studies of Long-eared Owl diet in the Mediterranean basin and the adjacent temperate zone to examine the geographical pattern of predation on bats. We predicted that occurrence of bats in the Mediterranean sites would be higher than in temperate sites of similar latitude because (1) rodent abundance undergoes pronounced seasonal and annual fluctuations, and owls must search for alternative prey and (2) the season of bat activity is longer, and bat average abundance higher, in warmer Mediterranean environments (Avery 1985, Altringham 1996).

Methods

We studied food habits of Long-eared Owls in Devesa de l'Albufera, one Mediterranean coastal site near Valencia city, Spain (39°21′N, 0°19′W). The owl habitat is a mosaic of pine forest (*Pinus halepensis*) with dense understory and open areas, mostly dunes and mesic interdune depressions (Costa et al. 1982). This forested landscape is highly disturbed (many buildings and regular recreational activities) and surrounded by a large expanse of rice fields. From November 1995 to June 2003, we collected owl pellets from beneath roost and nest sites on a monthly basis. We identified prey remains and, for each pellet, determined occurrence and minimum number of individuals of prey species. Using these data, we analyzed spatio-temporal fluctuations in bat predation. For analysis of seasonal variation in bat consumption, seasons were defined as winter (January–March), spring (April–June), summer (July–September), and fall (October–December).

We carried out the biogeographic comparison of bat predation using data from 30 diet studies from southern Europe (Table 1). Each study area was assigned to the Mediterranean or the temperate climate region according to Emberger et al. (1963; Fig. 1). We excluded northern temperate localities to avoid diets almost completely dominated by voles. For diets containing bats, we used Spearman correlation analysis to test the hypothesis that proportion of bats decreased with increasing latitude and altitude.

Results and Discussion

Bat Consumption in Devesa de l'Albufera, Coastal Spain. We collected 2012 pellets that contained 6210 prey items. Pellets containing bat remains originated mainly from a communal roosting site (60%) and also near 16 nest sites, where we recorded successful owl reproduction. Bats accounted for 2% of prey items (Table 1), which is the largest percentage thus far reported for Long-eared Owls (Marti 1976, Mikkola 1983; Table 1). Of 126 bats, 124 were pipistrelle bats (*Pipistrellus* spp; Table 2). Bat remains occurred in all seasons, but predation on bats was significantly higher during the peak of bat activity and abundance in spring and summer ($G = 47.3$, df = 3, $P < 0.001$; Fig. 2). In our study area, the first flights of young pipistrelle bats take place between mid-July and mid-August (D. Almenar and M. Monsalve pers. comm.), and during the initial 2 wk their flight skills are less than those of adults (Blanco 1998). Thus, the combination of the annual peak in abundance associated with the emergence of young bats and their relatively higher vulnerability, associated with their reduced flight capability, may help to

Table 1. Long-eared Owl diet composition in 30 localities of southern Europe. Each locality is assigned to a climatic region either Mediterranean or temperate. The percentage of bats, rodents, and other prey are calculated on the total number of prey individuals. Numbers assigned to each study area are the same as in Fig. 1.

STUDY	COUNTRY	CLIMATIC REGION[a]	NO. OF PREY	PERCENT BATS	PERCENT RODENTS	PERCENT OTHER PREY	SOURCE
1	Spain	M	874	0.00	86.61	13.26	Alegre et al. 1989
2	Spain	M	232	0.00	96.10	3.90	Delibes et al. 1984
3	Spain	M	6929	0.04	90.70	9.20	Araújo et al. 1974
4	Spain	M	3726	0.00	92.60	7.30	San Segundo 1988
5	Spain	M	3185	0.03	78.50	21.50	Veiga 1980
6	Spain	M	255	0.00	96.50	2.80	López-Gordo et al. 1977
7	Spain	M	804	0.00	72.60	27.40	Amat and Soriguer 1981
8	Spain	M	6210	2.03	52.77	45.20	This study
9	Spain	M	6249	0.08	89.00	10.70	Corral et al. 1979
10	France	M	368	0.00	58.40	39.13	Kayser and Sadoul 1996
11	Italy	M	494	0.00	90.08	9.72	Gerdol and Perco 1977
12	Italy	M	121	0.00	95.87	4.13	Gerdol and Perco 1977
13	Italy	M	103	0.00	54.37	45.63	Gerdol et al. 1982
14	Italy	M	1157	0.00	93.52	6.49	Casini and Magnani 1988
15	Italy	M	181	0.00	97.24	2.76	Capizzi et al. 1998
16	Italy	M	338	0.30	98.20	1.50	Plini 1986
17	Italy	M	1787	0.00	81.60	18.50	Guidoni et al. 1999
18	Italy	M	201	0.00	95.10	5.00	Capizzi and Luiselli 1996
19	Italy	M	—	0.11	70.70	28.40	Sublimi and Scalera 1991
20	Italy	M	234	≤1.40	93.60	5.00	Sarà 1990
21	Greece	M	961	0.30	87.90	11.70	Alivizatos and Goutner 1999
22	Italy	T	1787	0.00	81.60	18.40	Bertolino et al. 2001
23	Italy	T	1836	0.00	85.52	14.44	Galeotti and Canova 1994
24	Italy	T	519	0.00	83.63	16.37	Mezzavilla 1993
25	Italy	T	655	0.00	93.44	6.56	Malavasi 1995
26	Italy	T	593	0.00	90.58	9.42	Aloise and Scaravelli 1995
27	Italy	T	98	0.00	79.59	20.40	Riga and Capizzi 1999
28	Slovenia	T	10991	0.00	95.48	4.52	Tome 2003a
29	Romania	T	1268	0.00	88.18	11.82	Marariu et al. 1991
30	Switzerland	T	4639	0.00	99.23	0.77	Roulin 1996

[a] M = Mediterranean and T = temperate region.

explain the high occurrence of bats in summer samples. The relative importance of bats in the diet varied by year (G = 79.3, df = 6, $P < 0.001$; Fig. 2). In our study area and other Mediterranean environments, rodent populations typically show annual minima during summer, especially during warm years (Blondel and Aronson 1999). Although owl consumption of rodents roughly follows availability (Fig. 3), bat predation was unrelated to the proportion of rodents in the summer diet (r_s = 0.048, N = 8, P = 0.911; Fig. 3). This suggests that bats are not specifically sought as an alternative prey. The hypothesis that bats are taken only in years of marked rodent scarcity also predicts a clumped occurrence of bats in the diet over the 8 study yr. However, bat occurrence during 31 successive seasons did not differ from a random sequence (runs test, Zar 1984; Z = 0.726, P = 0.233; Fig. 3).

Bat remains occurred in 42 pellets (2.1%). In 27% of these, bats were the only prey item, with 2–8 individuals per pellet. In 62% of pellets, bats occurred together with other prey, but accounted for ≥50% of prey items in each sample. The distribution of the number of individual bats per pellet was aggregated (did not fit a Poisson distribution with λ = 0.055, χ^2 = 42.62, df = 1, $P < 0.001$; only pellets with bats, λ = 2.643, χ^2 = 13.23, df = 3, P = 0.004). These results suggested that bats were clumped when captured. Pipistrelle bats are

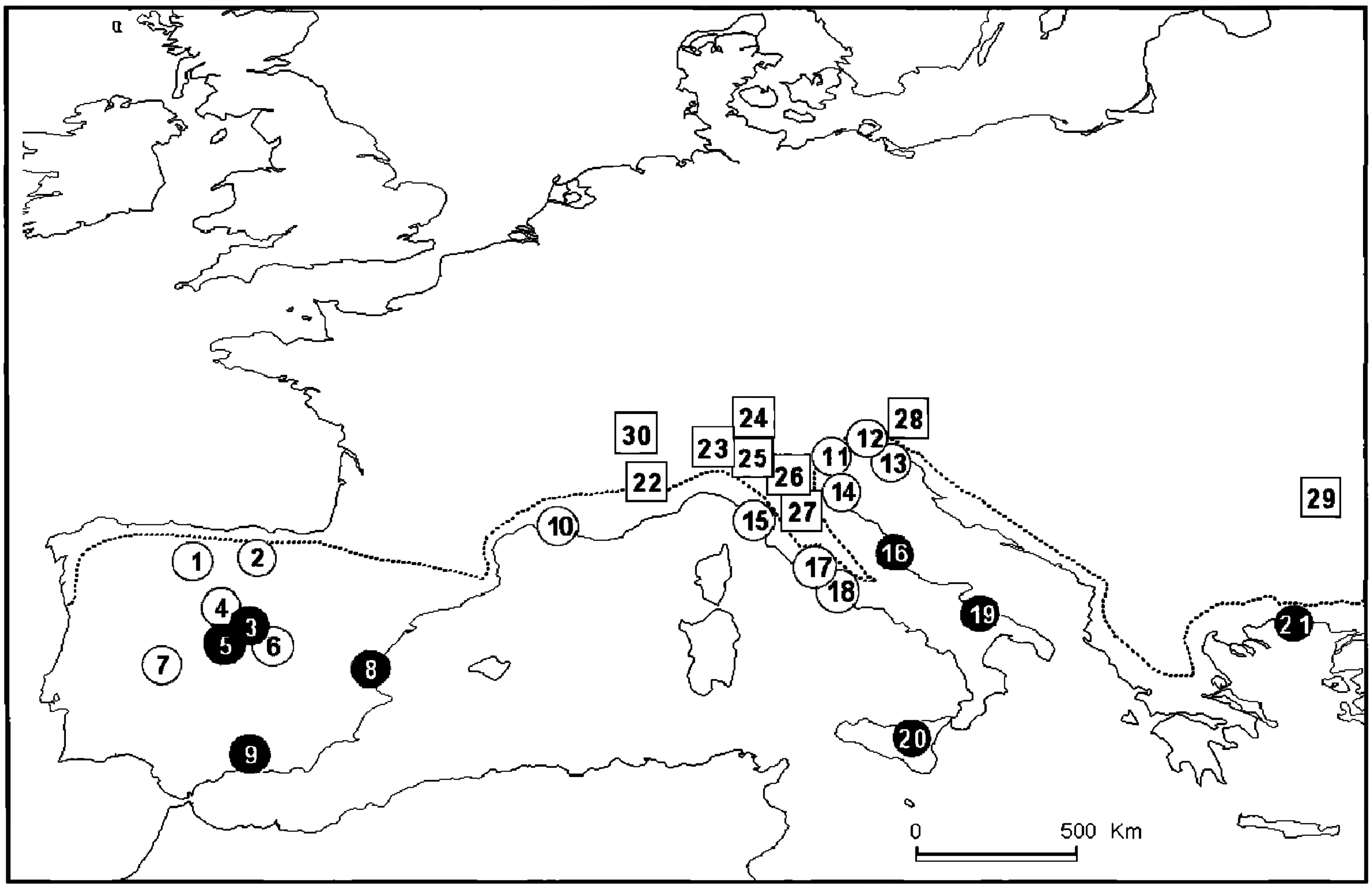

Figure 1. Localities where Long-eared Owl diet was studied in southern Europe. The broken line separates the temperate (squares) and the Mediterranean localities (circles) following Emberger et al. (1963). Black circles indicate sites where bat predation has been recorded. Numbers correspond to study numbers in Table 1.

Table 2. Bat species in the diet of Long-eared Owls in the Mediterranean region of Europe. Seasons when predation occurred and the range of body mass (g) are also shown. Body masses are from Palomo and Gisbert (2002). Study number and location are as in Table 1 and Fig. 1.

Species	Body Mass (g)	Season	Source	Study
Greater horseshoe bat	14.6–31.6	Winter	Alivizatos and Goutner 1999	21
(*Rhinolophus ferrumequinum*)		All seasons	This study	8
Greater mouse-eared bat	21.0–35.0	Winter–Spring	Corral et al. 1979	9
(*Myotis myotis*)		Fall	Sublimi and Scalera 1991	19
Lesser mouse-eared bat (*Myotis blythii*)	18.0–29.5	Spring–Summer	Veiga 1980	5
Whiskered bat (*Myotis mystacinus*)	4.0–8.0	All seasons	Plini 1986	16
Myotis spp.		Winter	Alivizatos and Goutner 1999	21
Pipistrellus spp.	3.5–10.0	All seasons	This study	8
Serotine bat (*Eptesicus serotinus*)	14.0–33.0	Winter–Spring	Corral et al. 1979	9
Brown long-eared bat (*Plecotus auritus*)	6.8–12.0	Spring–Fall	Araújo et al. 1974	3
Schreibers' bat (*Miniopterus schreibersii*)	10.1–20.8	All seasons	This study	8
European free-tailed bat (*Tadarida teniotis*)	22.0–54.0	Winter	Alivizatos and Goutner 1999	21

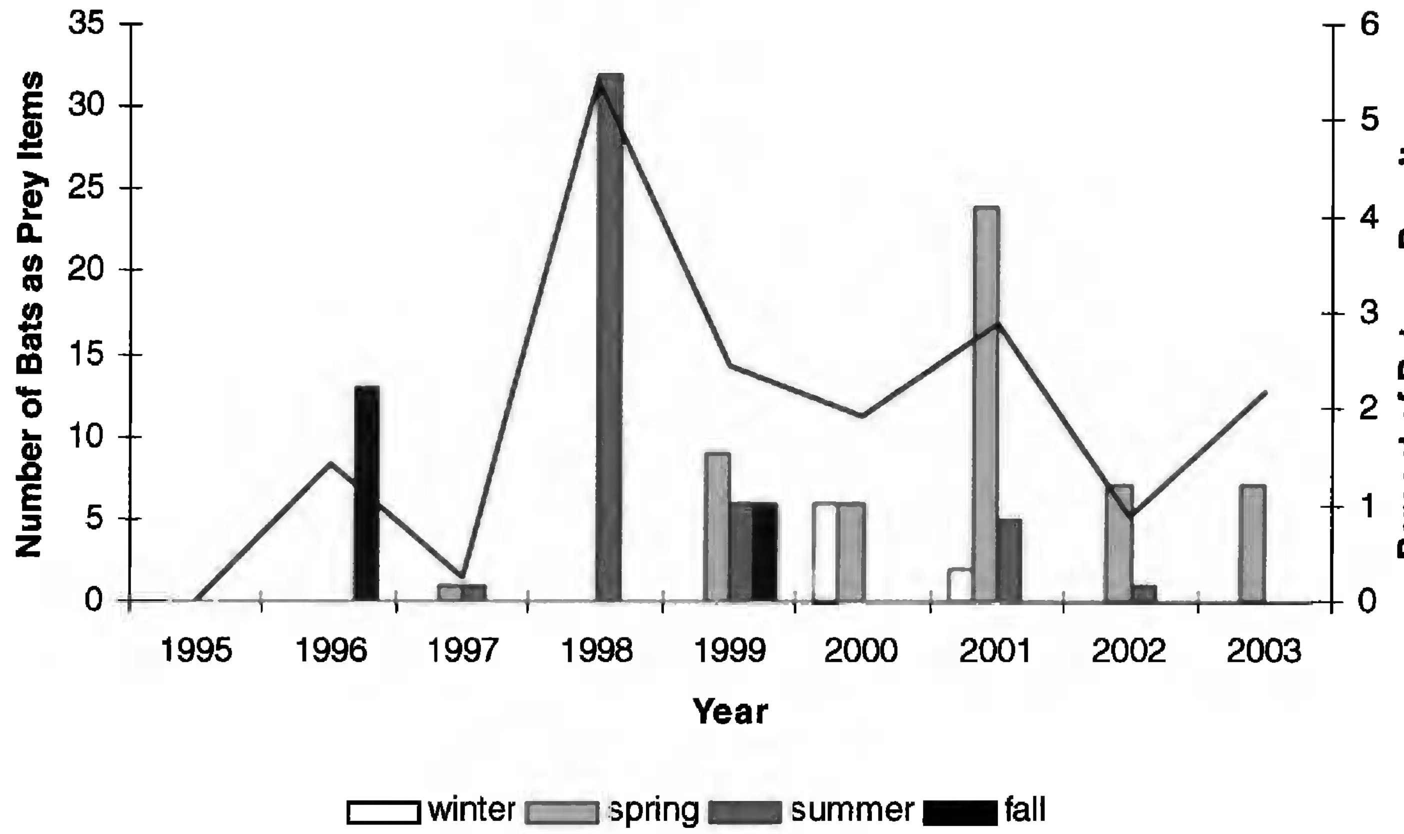

Figure 2. Temporal variation in the number of individuals taken by Long-eared Owls (bars) and in the percent of bats in terms of the total number of prey items (line) in Devesa de l'Albufera between 1996 and 2003.

very abundant in the study area and roost in colonies, often in buildings. Long-eared Owls could capture them at emergence as pipistrelle bats leave the roosts in large groups, but return as single individuals or in small groups and much more spaced over time. Although pipistrelle bats do not gather while foraging over large rice fields, they can form large aggregations when feeding along

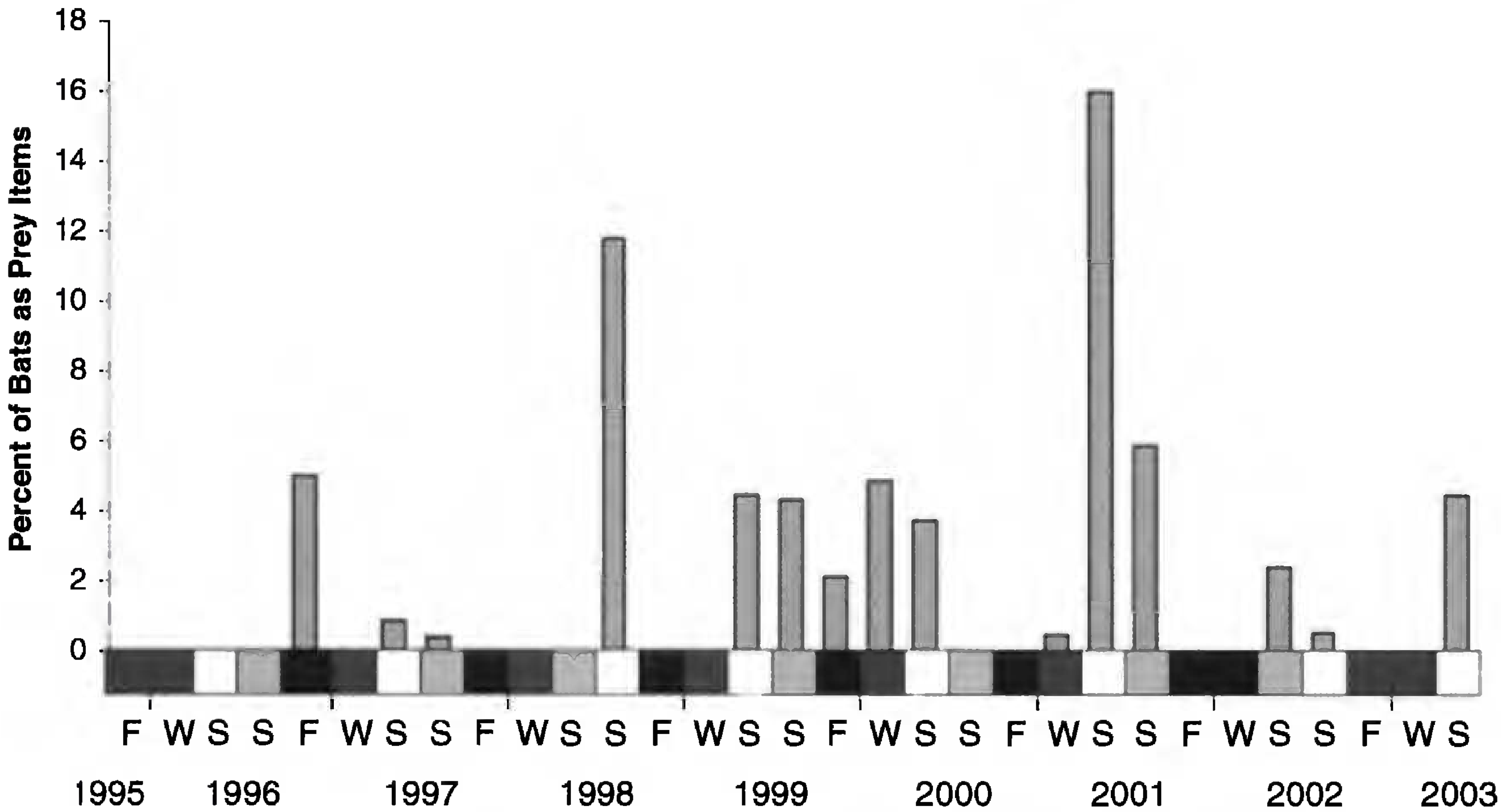

Figure 3. Seasonal variation in the percent (on the total number of prey items) of bats taken by Long-eared Owls in Devesa de l'Albufera between 1995 and 2003. Below the bars and for each year, shading intensity of cells indicates the ranked percentage of rodents in the diet, from the highest (dark) to the lowest importance (light) in the seasonal diet.

drainage channels or near street lamps (Blake et al. 1994), and the owls could hunt them there as well. Predation by nocturnal raptors on predictable accumulations of bats has been previously documented (Barclay et al. 1982, Fenton et al. 1994, Hoetker and Gobalet 1999).

The spatial distribution of bat remains during the owl breeding season was not random. Bat remains appeared in pellets from only five ($N = 205$ prey items) of 16 nests sampled. The mean percentage of bats per positive nest sample was 17.6 ± 13.0% (SD) of prey items. Only in one owl nest did bats account for <11% of prey, and the maximum observed was 37%. These figures make less plausible the idea of an opportunistic capture of bats as a result of accidental encounters (Ruprecht 1979). Our results were consistent with the hypothesis of individual differences in ability to catch bats or with individual knowledge of the location of pipistrelle colonies, which may be more profitable to exploit than solitary bat species if the emergence of large numbers of bats increases hunting success (Fenton et al. 1994). Even small-sized pipistrelle bats (body mass = 7.5 g) could be a profitable prey for Long-eared Owls if available in large quantities. The biomass of 8 pipistrelle bats (60 g; the maximum number of bats found per pellet) may satisfy two thirds of the daily energy needs (93.3 g for a 280 g owl; Wijnandts 1984), perhaps with little energy expenditure during foraging.

Biogeographic Pattern. We considered 21 diets for the Mediterranean region (34 410 prey items) and nine diets in the adjacent temperate region (22 386 prey items; Fig. 1). In the Mediterranean region, 38% of diets included bats as prey, whereas bats did not occur in any diet for the temperate region (Table 1). These differences in bat occurrence were significant ($G = 6.885$, df = 1, $P = 0.009$). Even excluding our study in coastal Spain, where we found an unusually high quantity of bat remains, the mean proportion of bats in the Mediterranean diets was significantly higher than in the diets of adjacent temperate sites (Mann-Whitney U-test, $Z = 1.98$, $P = 0.048$). In the Mediterranean region, the overall importance of bats in the diet of Long-eared Owls (0.43% of prey-items) was at least twice as high as in other geographical areas. But the large number of bats in the diet of owls in our study area was very influential in this comparison. In fact, omitting our results from eastern Spain, bats only represent 0.06% of prey items found in the combined diets from the Mediterranean region, which is similar to figures found elsewhere. In the diets from North America (23 888 prey items) and temperate Europe, plus Iraq, reviewed by Marti (1976), bats did not occur. In later reviews, Mikkola (1983) and Speakman (1991) found that bats accounted for <0.20% of prey items in Europe (67 805 prey items) and 0.05% in the British Isles (12 870 prey items).

In the studies we reviewed, bat predation was restricted to latitudes 37–43°N and altitudes 0–1400 m. Differences between localities in bat occurrence in the diet could not be attributed to a decline in bat species richness northwards, as species richness is almost constant at latitudes 35–50°N in Europe, which encompass all localities in Figure 1 (Pérez-Barbería 1991, Mitchell-Jones et al. 1999). However, bat abundance increases with decreasing latitude and altitude (Pérez-Barbería 1991, Kunz and Fenton 2003). Moreover, following the temporal pattern of insect availability, bats in Mediterranean environments show an extended activity season (Avery 1985, Altringham 1996, Blondel and Aronson 1999). Indeed, bat predation occurs in all seasons (Table 2). If an extended period of activity and a higher abundance were indicators of increased availability of bats for owls, we would expect increasing bats in the diet with decreasing latitude and altitude. We found no such correlations (latitude, $r_s = -0.05$, $P = 0.91$; altitude, $r_s = -0.45$, $P = 0.26$), but these analyses were based on small sample sizes ($N = 8$ diets containing bats).

Long-eared Owls preyed on nine of 29 bat species present in southern Europe (Mitchell-Jones et al. 1999; Table 2). Speakman (1991) suggests that large bat species would be more profitable prey than small ones, and therefore selected by raptors. However, Long-eared Owls consumed a variety of bat species, very different in body size, and there was no bias toward large species (Table 2). All the bat species that owls consumed, except *Tadarida teniotis*, forage low in open areas (Altringham 1996), just as Long-eared Owls do (Mikkola 1983, Tome 2003b) while hunting terrestrial prey on the wing (Marks et al. 1999). Excluding our results in coastal Spain, in Mediterranean environments, mean bat intake per diet, standardized as bats per 1000 prey items, was 3.4 individuals, suggesting that predation is in most cases opportunistic (Ruprecht 1979). Comparable results have been obtained for Barn Owls (*Tyto alba*; Pérez-Barbería 1991), which are regarded as opportunistic predators of bats.

We conclude that bat aggregations could be a locally important food source for some individual owls during certain periods, as exemplified by the population of Devesa de l'Albufera. More generally, this evidence supports the view that Long-eared Owls may show substantial trophic plasticity, in contrast to their widespread recognition as a rodent specialist. In other words, their trophic response may be context-dependent rather than imposed by morphological or behavioral constraints that typically affect all populations across the range of true specialists.

At the geographical scale, bat abundance does not seem to reflect bat availability for Long-eared Owls, maybe because hunting strategies for preferred prey such as rodents are not compatible with a regular exploitation of flying bats. Accordingly, bats occur in a number of diets across the Mediterranean region, but their contribution remains largely irrelevant.

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